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THE DEVELOPMENT OF A GAMEBIRD RESEARCH STRATEGY: UNRAVELING THE IMPORTANCE OF ARTHROPOD POPULATIONS

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ABSTRACT

This paper describes work conducted in the United Kingdom (UK) on upland gamebirds, primarily gray partridge, that identified the importance of arthropod abundance in determining chick survival and in the overall population dynamics of this declining quarry species. Several sequential steps that were taken to quantify the importance of arthropods in determining levels of chick survival, ranging from laboratory studies with captive chicks, through field-based surveys to computer simulation are described. Next, various field-scale experiments to manipulate vegetation to increase arthropod densities are described. These included the management of cereal crop edges with reduced levels of pesticides.

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INTRODUCTION

The importance of arthropods in the diet of gamebirds, especially to young chicks, has been quantified by many studies throughout the world. In many species this importance has been considered crucial in determining levels of chick survival, for example in red grouse (*Lagopus lagopus scoticus*) (Savory 1977, Hudson 1986), black grouse (*Tetrao tetrix)* (Baines 1996), capercaille (*Tetrao urogallus)* (Baines et al. 1994) and ring-necked pheasant (*Phasianus colchicus*) (Hill 1985). In other studies, rates of chick survival and the importance of arthropods have been shown to be the key factor (Varley and Gradwell 1960) in determining annual variations in population densities, for example, in the gray partridge (*Perdix perdix*) (Blank et al. 1967, Potts 1986).

However, it would be fair to say that, historically, these studies that explored the relationships between gamebirds and arthropods have been primarily undertaken in Europe. For example, Potts (1986) cataloged studies of gray partridges where the crop contents of chicks had been examined to determine at least the numerical dominance of arthropod species in the chick diet. Such studies had been conducted in western Europe (Britain, France and Denmark) and eastern Europe (Poland, Hungary, Czechoslovakia and the Soviet Union).

In North America, studies of gamebird populations have tended to focus on problems associated with nesting cover and winter survival. However, as early as the 1930's biologists noticed the importance of insects in the diet of northern bobwhite quail chicks (*Colinus virginianus*) (Stoddard 1931). However, only recently have North American workers begun to focus on problems associated with arthropods and the role they play in determining levels of chick survival. Notable exceptions to this bold statement were studies reported at the Third National Quail Symposium (Quail III) held in 1992.

Workers in Kansas (Taylor et al. 1993), Florida (DeVos and Mueller 1993) and Missouri (Dailey and Seon 1993) reported work on arthropods. The most detailed work was reported from Missouri by Burger et al. (1993). This growing interest was also reflected in the strategies for quail management outlined at Quail III which stated the need "to determine the indirect effect of pesticides on quail populations" (Capel et al. 1993). Five years later, at the Fourth National Quail Symposium (Quail IV) arthropod studies were again reported by the same groups or researchers, most notably in Florida (Palmer and Bromley *this volume*) and Mississippi (Carver et al. *this volume*).

Little information is available on the insect diet of the chicks of quail species other than northern bobwhite. Furthermore the insect dietary studies already conducted for northern bobwhites scarcely cover the full extent of the inevitably large variations to be encountered in a species with such an extensive range in North America. Land use and climate variations in a species in habitats from Florida to southern Ontario, from Texas to Massachusetts and from intensive row crop farming in Iowa to timber plantations in Georgia will be large (Church et al. 1993). For those about to embark on researching relationships between quail chick survival and arthropod abundance, this paper therefore draws upon the experiences of British researchers and their studies on gray partridge chick survival, arthropod ecology and management of brood cover for insects consumed by chicks. Six approaches are described that have led to our understanding of insect-gamebird chick interactions.

Table 1. Effect of diet on the daily growth rates of partridge chicks (from Cross 1966).

	Average weight gain (% per day)	
	Gray Partridge (n = 45)	Red-legged Partridge (n = 60)
Starter crumb	11.0	17.0
Insects	6.0	12.0
Plant material	0.5	1.0

APPROACH 1. LABORATORY FEEDING TRIALS

In feeding trials, partridge chicks were fed various diets to investigate the role of insects in the growth of chicks, especially in relation to feather development. Batches of chicks were fed a high protein weed mixture comprising grass weed spikelets (*Poa annua*), and buds of forage legumes, especially clover and weed seeds of the genus *Polygonum* (a known component of adult diets) (Pulliainen 1966). Other chicks were fed insects collected from nearby cereal fields. Control batches of chicks were fed high protein poultry starter crumb and all chicks were fed quantities of particular diets *ad libitum* along with supplies of grit and water.

Growth rate was found to be greatly influenced by food type; those feeding on plant food grew so slowly that it was barely measurable. Chicks fed on insects grew much faster (Table 1).

Cross (1966) considered certain amino acids, particularly methionine and cystine to be particularly important for feather growth. Wise (1982) calculated availability of these two amino acids in the dry matter content of various foods for red grouse and found insects contained a greater percentage of available methionine and cystine than did vegetable sources (grass, beans, wheat) or even from meatmeal.

APPROACH 2. GUT DISSECTION

Direct evidence of the diet of young chicks was obtained from samples of chicks collected from the field and by examination of their crops and gizzards. Forty gray partridge chicks were obtained from an extensive study area of farmland in southern England over a 9-year period. Chicks were aged and food items removed from their crop and gizzards. Invertebrates, seeds and plant material were identified and counted under a binocular microscope.

During the first week, gray partridge chicks fed primarily on small invertebrates, (particularly cereal aphids, homopterans and Collembola), Coleoptera (particularly Curculionidae and Chrysomelidae) and sawfly larvae (Hymenoptera: Tenthredinidae) (Table 2). In contrast, after this first week, ants, a hitherto absent group became the most numerous dietary item followed by cereal aphids, Chrysomelidae and hemipterans (particularly Miridae). After the first week sawfly larvae and Collembola were rarely taken. At less than a week old, 95% (by item) of the diet of chicks were invertebrates. Up to 21 days old this proportion decreased to 48%.

Table 2. Numbers of invertebrates, plant seeds and leaves found in the crops of gray partridge chicks in the 1970's in southern England (from Vickerman and O'Bryan 1979).

	Age	
	1 week	1–6 weeks
Invertebrates		
Arachnida	22	40
Mollusca	6	3
Hymenoptera: Parasitica	18	25
Formicidae	0	2565
Tenthredinidae	34	1
Diptera	18	34
Coleoptera	77	188
Hemiptera: Cercopidae & Aphididae	63	717
Hemiptera: Miridae	4	113
Lepidoptera	6	24
Collembola	61	32
Others	4	44
Total Invertebrates	313	3786
Plant material		
Monocot. Seeds	12	2909
Dicot. Seeds	3	963
Leaves	2	267
Total Plant Material	17	4139
% invertebrate food	94.8	47.8
% plant food	5.2	52.2

Most chick mortality occurs during the first few weeks after hatching and peaks during the 10-day period of maximum dependence of insects (Potts 1986). Church (1986) estimated daily mortality to be 2.1% per day for the first 10 days and 0.5% per day from 10 to 74 days. A comparable study by Enck (1986) found the daily mortality rates to be 1.6% and 0.3% for the same age intervals.

Green et al. (1986) observed that gray partridge chicks <10 days old were unable to grind open grass seeds in their gizzards even though they were able to ingest such material. In contrast, red-legged partridge chicks could extract protein from weed seeds at 3 days old and gut dissection showed a plant and invertebrate composition in the diet of week old chicks of 72% and 28% (Vickerman and O'Bryan 1979). In tests with ant pupae dyed with vegetable coloring it was found that gray partridge chicks preferred green to yellow and green and yellow to blue, red or black (Vickerman and O'Bryan 1979). It also appeared that green insects occurred in chick diet more often than expected from their abundance in brood-rearing areas e.g., cereal aphids, Collembola, Miridae and sawfly larvae.

APPROACH 3. FAECAL ANALYSIS

Considerable expertise has now been developed to identify arthropod food items of galliform chicks, particularly gray partridges, from the fragments of exoskeleton remaining in their faecal material. This method has the advantage of being non-destructive and can readily be carried out as a adjunct to radio telemetry studies (Moreby 1988). Faecal material can easily be collected from roost sites located by telemetry and insect fragments identified by comparison with reference to a collection of species collected from the previous day's foraging areas. Preferred insects can also be identified in this manner by comparing presence in faecal samples with their relative abundance in brood-rearing areas. In general, insects are considered preferred when they occur more than twice as frequently in faecal samples as in vacuum insect net samples from the field where the faeces were collected (Green 1984). In studies reported at Quail III (Sotherton et al. 1993) following a multiple stepwise regression, there was a significant positive relationship between gray partridge chick survival per brood to 21 days old and the proportion (percentage) of sawfly larval and Chrysomelidae adult and larval fragments in the total arthropod fragment composition of chick faecal samples collected from roost sites (r = 0.78, 7 = df, $P < 0.05$). In a sample of 17 radio-tagged ring-necked pheasant hens 55% of the variation in chick survival was accounted for by the proportion of Heteroptera, sawfly larvae and Staphylinidae larvae in chick droppings (Sotherton et al. 1993).

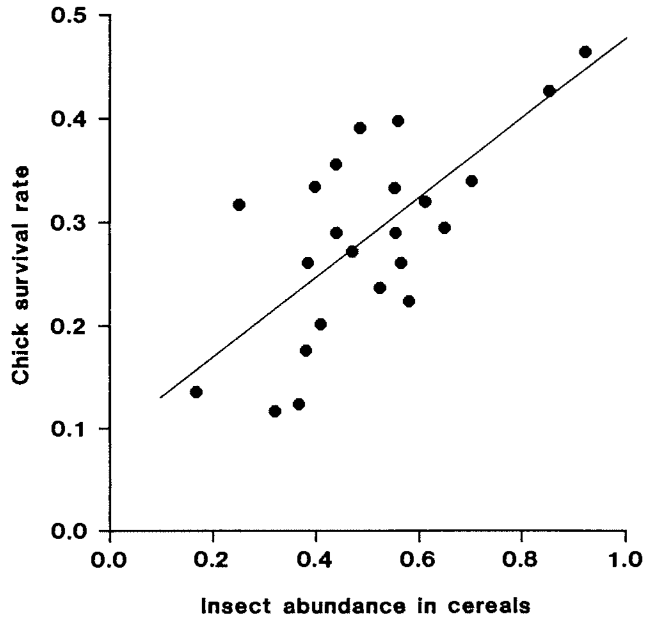

Fig. 1. Relationship between gray partridge chick survival (to 6 weeks) and chick-food insects taken from Sussex Study area 1970–1992 (from Aebischer, 1997).

APPROACH 4. CORRELATION

The Game Conservancy Trust has been collecting data on gray partridge chick survival in relation to the abundance of insects since 1968 in an attempt to investigate causes for the decline of this species in the UK. This research was carried out on 62km^2 of farmland on the Sussex Downs in southern England. Since 1970, annual counts of partridges have been made each year and insect abundance in cereal fields is measured on over 100 fields every June. Full details of this long-term monitoring project appear in Potts and Aebischer (1995).

Several sources of field data support the link between chick mortality and insect abundance. Evidence from faecal analysis has already been described. Annual chick survival rates from the Sussex study are positively correlated with an index of insect abundance in cereals obtained in the summer (Figure 1) (Aebischer 1997). The calculation of this index is explained later.

The introduction of Geographical Information Systems analysis has enabled the Sussex data to be mapped by field by year. The results of the annual gray partridge surveys from 1970 to 1994 were transferred to a computerized database, MAPINFO 3.0 (MapInfo Corporation, Troy, New York). The following series of maps of the abundance of caterpillar-like larvae (both lepidopterans and sawfly larvae) during June, and gray partridge coveys in the autumn for 1970 and 1994 shows the spatial correlation of broods to insects (Figures 2a–2d). These correlations are most pronounced in the more recent years after insect populations had declined on farmland subjected to increasing levels of intensified production technology (sawfly larvae by over 50% in 25 years, Aebischer 1991).

APPROACH 5. MULTIPLE REGRESSION

With such an extensive spatial and temporal database, we have been able to carry out multiple regression analyses to partition causes of annual chick survival. Multivariate regression models of chick mortality using weather as the dependent variable and different measures of insect abundance as the independent variables, were constructed. The insect data from the annual monitoring in Sussex and weather parameters from 10 June to 10 July each year were used. For the period from 1969 to 1985 inclusive the earliest model using weather variables collected 5 miles south of the center of the study area was constructed. A total of 58% of the variation in chick mortality was explained as follows (Potts 1986).

$$\text{Chick survival rate} = 1.532 - 0.016x_1 - 0.048\,x_2$$

where x_1 = sum density of preferred insects (m^{-2}) in cereal crops in June

x_2 = mean daily temperature between 10 June–10 July.

For the data from 1970 to 1987 a forward stepwise multiple regression was used to predict chick survival rate from a model and identify the most important

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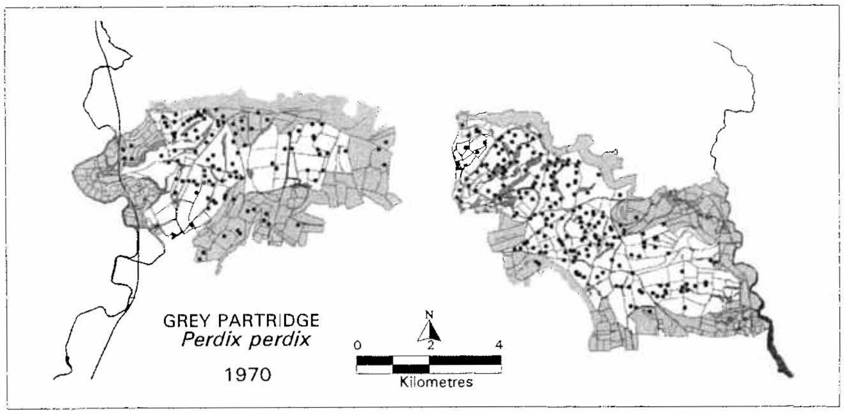
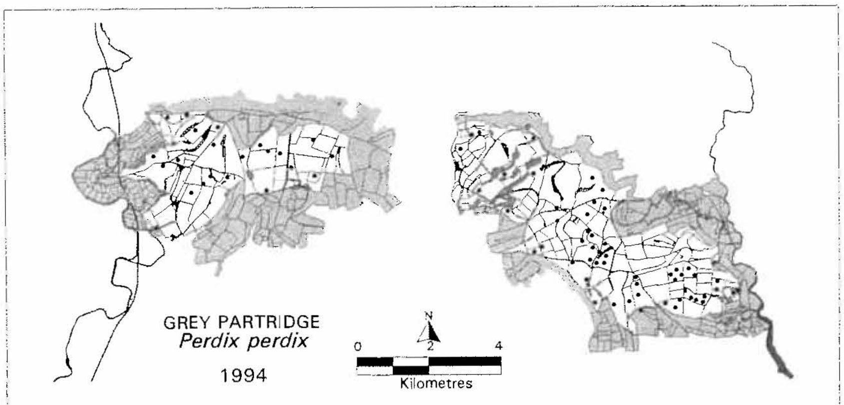
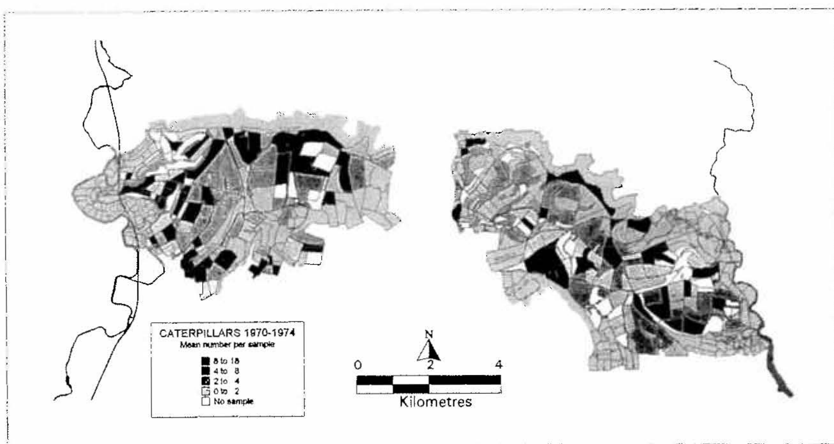
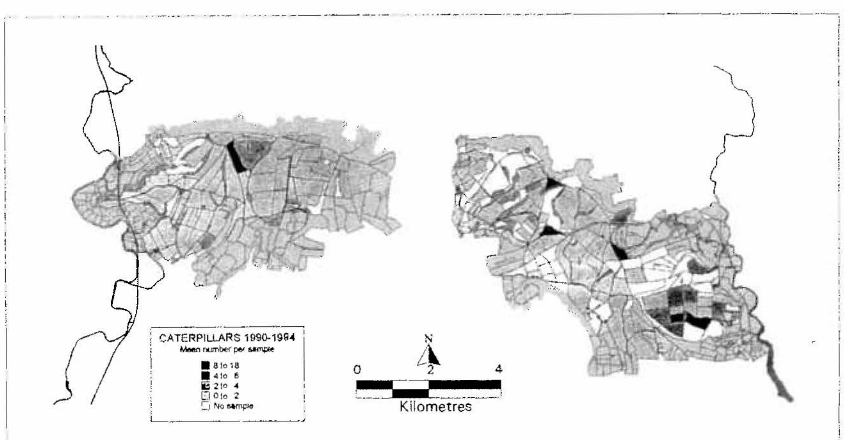
Fig. 2. (a) Gray partridge brood counts on the Sussex Study area, 1970. Each point represents a covey; (b) Gray partridge brood counts on the Sussex Study area, 1994; (c) Mean numbers per field of caterpillar-like chick-food insects sampled in cereal fields on the Sussex Study area in June between 1970 and 1974; (d) Mean numbers per field of caterpillar-like chick-food insects sampled in cereal fields on the Sussex Study area in June between 1990 and 1994.


GREY PARTRIDGE
Perdix perdix
1970
N
0 2 4
Kilometres


GREY PARTRIDGE
Perdix perdix
1994
N
0 2 4
Kilometres


CATERPILLARS 1970-1974
Mean number per sample
8 to 18
4 to 8
2 to 4
0 to 2
No sample
N
0 2 4
Kilometres


CATERPILLARS 1990-1994
Mean number per sample
8 to 18
4 to 8
2 to 4
0 to 2
No sample
N
0 2 4
Kilometres

chick-food groups. The following equation explains 52% of chick mortality (Potts and Aebischer 1991).

$$I = 0.141x_1 + 0.120x_2 + 0.083x_3 + 0.006x_4 + 0.0004x_5$$

where I = Index of insect abundance
x_1 = density of ground beetles (Coleoptera:Carabidae);
x_2 = caterpillar-like larvae;
x_3 = leaf beetles and weevils (Coleoptera: Chrysomelidae and Curculionidae);
x_4 = plant bugs and leaf hoppers (Hemiptera: Miridae and Cicadellidae);
x_5 = cereal aphids (Hemptera: Aphididae).

APPROACH 6. FIELD STUDIES

The approaches described so far represent a body of evidence which supports the hypothesis that gray partridge chick survival is dependent on the abundance of preferred chick-food insects in brood-rearing cover. The final approach sought to test this hypothesis in the field. Such tests have been carried out by controlled experiment and by circumstantial monitoring.

The first experiment describes the use of selectively-sprayed cereal crop headlands (field borders) now commonly known as Conservation Headlands to increase densities of chick-food insects at the edges of cereal crops. Radio telemetry data have shown these field borders to be the area most used by broods (Green 1984). Results of these experiments were presented at 2 North American gamebird symposia, both at Perdix V (Sotherton and Robertson 1990) and at Quail III (Sotherton et al. 1993). In summary, insecticides are excluded from the outermost edge of cereal crops (usually 6m wide) during the summer to preserve beneficial insects. Herbicides to control broad-leaved weeds are also excluded to provide host plants for these predominantly phytophagous insect species (Sotherton 1991).

Field experiments have demonstrated that the percentage weed cover in Conservation Headlands is over 4 times as high as in fully sprayed headlands, and that Conservation Headlands contain, on average, 3 times as many weed species (Sotherton 1991). In terms of insects, densities of the groups consumed by partridge chicks can be 3 times greater in Conservation Headlands than in fully sprayed headlands. The survival of partridge chicks follows suit: in each of 8 experimental years, the survival rate was higher where Conservation Headlands were present than where they were absent (Table 3). With Conservation Headlands, chick survival exceeded 30%, i.e., the minimum required to maintain a stable population (Potts 1986), in 5 of those years, whereas without Conservation Headlands it merely reached that level only during 1 year.

The field test of the hypotheses obtained by monitoring came from the annual counts of partridges and insects undertaken in the Sussex Study. Up until 1989, the use of insecticides to control cereal pests, particularly aphids in the summer, was slight. In 1989, for the first time, a broad-spectrum insecticide was applied to cereal crops across an entire farm (7km^2) to control aphids (Aebischer 1990). In all but 1 year between 1989 and 1995 (a 7-year period) most of the cereals on this farm were sprayed with insecticide up to 4 times per year. During these 7 years, the other farms on the study area either used no summer insecticides, or used much more specific aphicides (those less likely to kill chick-food insects or their insecticide use was very much less intensive). The study area could therefore be divided into 2 areas according to the intensive use of insecticides, (the 7km^2 area) and the other farms (21km^2). Chick survival rates (after Potts 1986) were calculated for each area each year, and compared between areas (paired t-test) in the periods before and during intensive insecticide use.

The annual chick survival rates on the intensive farm were lower in all 6 insecticide years than they were on the rest of the study area, whereas, before 1989, they had been higher in 16 out of 19 years ($X^2_1 = 7.28$, $P = 0.007$). On average, during these pre-insecticide years, the chick survival rate on the intensive farm was not higher than on the other farms ($t_{18} = 1.06$, $P = 0.303$). In contrast, the average chick survival rate was 22 ± 5% over the 6 insecticide years on the intensive farm, a third lower than on the other farms where it was 34 ± 3% ($t_5 = 3.53$, $P = 0.017$) (Table 4).

SUMMARY

The identification of the importance of insects in the survival of gamebird chicks, and the list of preferred insect species in the diet of chicks allows research to concentrate on the ecology of such beneficial insect groups, their requirements, and how they are able (or unable) to react to changes in agricultural practices. Only then can applied ecology begin to formulate management plans to increase their densities within brood-rearing areas for partridge chicks. In the UK, the example provided by the gray partridge and pheasant has led to the development of insect-rich Conservation Headlands and strategies to manage set-

Table 3. Percentage of gray partridge chicks that survived the first 6 weeks after hatching, in relation to the management of cereal headlands (outer 6m of the crop) on experimental farms in eastern England, 1984–1991, from Sotherton et al. (1993).

	Year							
Land use category	1984	1985	1986	1987	1988	1989	1990	1991
Conservation headlands	52%	22%	60%	46%	39%	48%	25%	21%
Fully sprayed headlands	27%	13%	28%	22%	25%	30%	23%	18%
Number of farms	8	8	9	11	12	9	20	18

Table 4. Mean chick survival rates (±1 Standard error, SE) on farms on the Sussex Study area before and during the intensive use of insecticides on 1 farm post 1989 (from Aebischer and Potts 1998).

	Chick survival rate (%)	
Years of study	Farms with slight or no insecticide use	Farms with intensive insecticide use (slight before 1989)
1970–1988 (n = 19)	27	34
SE	2	3
1989–1994 (n = 6)	34	22
SE	3	5

aside fallow areas to create high insect densities (Sotherton 1998).

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